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THE MICRODISTRIBUTION OF STREAM BENTHOS

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PROGRESS REPORT

THE MICRODISTRIBUTION OF STREAM

BENTHOS

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INTRODUCTION

The following Progress Report has been arranged in two general sections. The first is an abbreviated form of a manuscript to be submitted for publication to Ecological Monographs. The portions of the manuscript included in this report were selected to provide a fairly brief statement of progress achieved in certain areas of the project. The second section, consisting of five parts, presents, in appendix form, information not completely covered in section one. Even though the report is extensive, a tremendous amount of data have been omitted. For additional detail the following references can be consulted: Cummins et al. 1965, 1966; Cummins, 1966; Coffman, 1967; Cummins, 1968.

THE ECOLOGY OF A WOODLAND STREAM. I.
SPECIES COMPOSITION, STANDING CROP AND INGESTION
FOOD WEB OF THE FALL RIFFLE COMMUNITY¹

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INTRODUCTION

In recent years, interest in energetics of natural communities has grown rapidly; the area of stream ecology is no exception to this trend. Founded on several classical studies (Percival and Whitehead, 1935; Berg, 1948; Jones, 1950; Allen, 1951; Illies, 1956), the focus has been on individuals manipulated in the laboratory (e.g. Trama, 1957), populations (e.g. Waters, 1962), entire communities (Odum, 1957; Teal, 1957) or significant portions of them (e.g. Hynes, 1961; Macan, 1963; Minkley, 1963; Egglisshaw, 1964; Thorup, 1964; Minshall, 1965; Whilm, 1965; King and Ball, 1967). However, the gap between scant population data and a few "first order approximation" community energy budgets is obvious. (For additional review see Cummins, 1966.)

This paper deals with a portion of a long term study aimed at determining an energy budget for a lotic ecosystem, at the greatest level of detail feasible and employing the maximum possible amount of original data. The broad plan of investigation was conceived to consist of the following components:

- 1) determine community composition, standing crop fluctuations and an ingestion food web for the riffle portion of a natural stream ecosystem;
- 2) correct the ingestion trophic structure to an assimilation trophic structure;
- 3) determine production (growth and reproduction) and the assignment of maintenance costs (respiration) at the level of populations;
- 4) determine intra- (photosynthesis by periphytic algae) and inter-community (terrestrial and upstream contributions) supply of organic matter, as well as the loss (downstream) from the community;
- 5) prepare a "balanced" energy budget and relate it to criteria suitable for judging community stability;
- 6) establish a stable, semi-natural lotic system (stability to be judged on the basis of above criteria (5) and determine, under controlled conditions, energy flow (input, processing and loss) at a level of exactness not possible in completely natural systems;
- 7) conduct manipulative experiments relative to the relationship between community stability and energy flow.

Although at least initial estimates have been made in all seven categories, the results presented below are confined primarily to number one.

DESCRIPTION OF STUDY AREA

Linesville Creek is a small woodland stream, 8.9 kilometers in length, located in northwestern Pennsylvania (Crawford County) having a drainage area of 23 square kilometers. The woodland, riffle study area is located 2.7 kilometers from the mouth of the stream at Sanctuary Lake, the eastern arm of Pymatuning Reservoir (Cummins et al., 1968), an artificial impoundment of the Shenango River. During non-flood water

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conditions, the riffle sampling site is about 5.5 meters in width by 6 meters in length, with a maximum depth of about 0.25 to 0.5 meters and a flow velocity between 10 and 30 cm/sec.

The stream sediments are dominated by coarse particle sizes. The dominant sediment class ranged from 16 to 64mm (pebbles to cobbles). Calculated median phi diameters ($Md\phi$, see Cummins, 1962) ranged from -6 to -4. The drainage basin has a number of soil types, each owing its origin to the influence of the Wisconsin glaciation. Deposits of glacial drift of less than 50 meters are typical of the streams of Crawford County that meander through flood plains of Holly silt loam soil (Soil Survey, Crawford County, 1954). The water table is often less than 1 meter below the surface in such areas. The two most important physical aspects of the Linesville Creek drainage basin are the lack of relief and poorly drained soils, both primarily the result of the Wisconsin glaciation. The higher areas of the Linesville Creek drainage basin are dominated by Frenchtown and Wayne silt loams. The west bank of the Wallace Woods area, a 16 hectare woodland owned by the University of Pittsburgh and containing the Linesville Creek sampling site, contains three distinct soil types: Meadville silt, loam-sloping phase; Rittman silt, loam-sloping phase and Wayne silt, loam-steep phase. The east bank, a portion of which is cultivated is dominated by Meadville silt loam, an important soil type throughout the stream valley (U.S. Dept. Agriculture, Soil Survey, Crawford County, 1959).

The most common species of trees and shrubs growing along the stream are dogwoods (Cornus floridans and C. stolonifera), alders (Alnus spp.), willows (Salix nigra, S. spp.), viburnum (Viburnum spp.), river and yellow birches (Betula lenta and B. lutea) and hemlock (Tsuga canadensis). The common flood plain species of Wallace Woods, a 16 hectare woodland owned by the University of Pittsburgh which contains the Linesville Creek sample site, are black cherry (Prunus serotina), sugar maple (Acer saccharum), white ash (Fraxinus americana), american elm (Ulmus americana), apple (Malus sp.), basswood (Tilia americana), beech (Fagus grandifolia), black gum (Nyssa sylvatica), black, red and white oaks (Quercus velutina, Q. rubra and Q. alba), butternut (Jugulans cinerea), hawthorn (Crataegus spp.) and white pine (Pinus strobus).

Relative to the difficult problem of running water typology (Ber, 1948; Illies and Botosaneanu, 1963), the stream is classified as a marginal trout stream by the Pennsylvania Fish Commission, but presently supports no trout. According to Carpenter (1928), the study area of Linesville Creek is an intermediate between a "Troutbeck" and a "Minnow Reach". Based on the distribution of macrophytes the Butcher (1933) and Tansley (1939) systems would place it in a "Zone 1" category. According to Shelford's (1929) system, Linesville Creek is dominated by a Cladophora - Hydropsyche - Etheostomatinae type community, although a better description for the riffle section would be a diatom - Trichoptera, Chironomidae - Cottus community.

METHODS

Field Methods

Field sampling (Fig. 1) was restricted to a single riffle section in Linesville Creek from which a five sample transect was collected each month for 26 months (1964-1965). Samples were taken 0.5 meters apart along a transect line, with one sample from each margin (nos. 1 and 5), one at the center (no. 3) and two at intermediate positions (nos. 2 and 4) between the margins and the center of the stream. A specially designed riffle sampler (Fig. 2) was utilized to collect approximately 900 cm³ sediment samples (900 cm² to a depth of 10cm; sediment dry weights ranged from 3.2 to 17.0 Kg). The sampler, constructed of plexiglass, has a 25cm flange to which is glued a 10cm thick layer of sponge rubber. Once the sampler has been positioned on the stream bottom, two collectors kneel opposite one another on the flange which presses the sponge rubber against the riffle substrate, shutting off the water flow (Cummins, et al., 1966; Coffman, 1967).

Prior to sediment removal, three substrate units were selected for periphyton collections. The samples were biased in an attempt to approximate maximum standing crops of epiphytic algae by selecting sediment particles for sampling that supported

visibly dense growths. A specially designed sampler was employed to obtain algal scrapings 1cm^2 in area. A small, replaceable wire brush was used to remove the periphyton from the rock surface and a suction attachment pumped the sample into a collection vial.

After the three periphyton samples had been collected, the sediments were scooped out by hand. To account for large cobbles only partially in the sample area, such overlap was collected from two sides of the sampler and allowed to remain in place on the other two sides. After the sediments were removed to a depth of approximately 10cm, as determined by the dimensions of the largest unit within the sample area, the silt, sand and gravel remaining was stirred vigorously and the sediment suspension removed with a 0.064mm mesh dip net shaped to fit the inside dimensions of the sampler.

Current velocity was measured in the sampling area near the substrate - water interface with a pigmy current meter (Corbett, 1955). Oxygen concentration, pH, alkalinity and free CO_2 were measured occasionally during the study and found to vary over rather narrow ranges. A single analysis of trace elements revealed moderate nitrogen and phosphorous levels and low iron and silicon.

Laboratory Methods

The samples were taken immediately to the laboratory for rough sorting (Fig. 1). Each was thoroughly washed, rock by rock and the elutriated material trapped on a 0.49 screen (0.25 screen was also used during the second year of sampling). The animals collected in this manner were preserved in 70% ethanol plus 15% formaldehyde (the latter was required to prevent deterioration of gut contents). The same preservative mixture was added to the substrate and animals not removed in the washing process; fine hand sorting was accomplished over a period of several days.

Once the animals had been removed from the sediments, they were sorted to the lowest possible taxonomic category. Identifications were made with a dissecting microscope (maximum magnification 100X) or, in the case of many midge species, with a compound microscope (max. magnification 1500X). Sorting of samples to species was facilitated by the use of a habitat specific key, providing for the separation of 150 taxa, which had been developed over the course of several years prior to the initiation of quantitative sampling. (Available in mimeographed form from the authors upon request.)

After the taxa had been sorted, each animal was measured and placed in one of five size classes; in some instances these corresponded to instars (e.g. the Trichoptera) or groups of instars while in others they were merely arbitrary divisions. When possible, sclerotized head parts were measured. Size classes of Plecoptera, Ephemeroptera, Trichoptera, Megaloptera and Coleoptera species were determined on the basis of head capsule width at the eyes (measured at 50X). Chironomid and simuliid dipteran larvae were sized on the basis of labial plate and mentum width respectively (at 100X). Other dipteran families were separated into size classes by various measurements: Tipulidae (except Antocha based on head width), Tabanidae and Empididae (=Hemerodromia) by total length in mm; Rhagionidae (=Atherix) by length of caudal filaments (50X); Psychodidae by head capsule width at the eyes (50X). The two decapod species were sized by measuring basal rostrum width in mm and the sculpin (Colius bairdii) according to total length. The size class criteria established for 158 taxa have been presented in detail elsewhere (Coffman, 1967; see Appendix II, Table 1). Measurements of each specimen were made except when thousands of individuals of a given species were present in a sample. In those instances animals were sized visually and approximately every 25th animal was checked within each group.

Following completion of size class determinations, gut contents were removed from representatives of each size class for slide preparation and examination. Gutting techniques varied with different species, but the general procedure has been described previously (Mecom and Cummins, 1964; Cummins et al., 1965 and 1966). The general method has been summarized in Fig. 3. Digestive tracts were removed by microdissection and their contents rolled, teased, or stripped out, care being taken to remove all gut wall and other external species material. The diameter of the filter (0.45 pore size) used to concentrate the distilled water dispersed gut contents and the number of individual tracts processed was varied to achieve preparations of relatively uniform density. If material was too dense, accurate counts were difficult to obtain due to clumping while

if too little material was used, sparse preparations resulted which were extremely time consuming to read. When too little material was available for preparation of even the smallest filter size, a "squash mount" was made by placing the gut material directly onto a slide and dispersing it with a cover slip. Care was taken to keep the material as concentrated as possible to facilitate reading. Such preparations were quite time consuming to process since proportional counts were not possible, due to the non-uniform area covered by the material, and the entire mount had to be enumerated.

As shown in Fig. 3, reading a gut preparation produced data on three food categories; total number of animals ingested (including their species and size), total number of algal cells counted by genus per a given area of filter (reported as linear mm read under oil); and number of detrital particles, recorded by maximum diameter, on a given area of the filter. As mentioned above, in the case of "squash mounts", total counts were made for all three categories and no further calculations were necessary. Great care was necessary to avoid confusion of gut wall fragments and stained sand grains with detritus. The semi-solid gut material found in Atherix variegata, Palpomyia sp and, on occasion, Eriocera fultonensis was interpreted as being partially solidified body fluids from prey, and not detritus. The most easily determined detritus was vascular plant tissue and fungal hyphae and spores.

The raw data were punched on cards and further calculation were accomplished by computer programming. The total amount of each category ingested was calculated as follows (see Fig. 3).

1) Total animals ingested was determined from head parts, tarsal and anal claws and other characteristic structures, and each size of each species multiplied by the appropriate dry weight and calorie equivalent stored within the program. A library of camera lucida drawings facilitated the identification of ingested animal fragments. Total weight and calories of animals ingested was determined by summation and expressed on a per individual basis. A value of 3950 cal/gm, determined from natural stream detritus was employed to convert detrital weights to caloric equivalents (Cummins, 1967; Coffman, 1967).

2) The number of algal cells counted per a given area of the filter was converted to the estimated number on the entire filter and the weight of diatoms calculated by multiplying number of cells by 8.34×10^{-6} gm, the average weight of a single cell. This value was modified from Trama's (1957) data on Navicula minutissima by obtaining an average cell volume for Linesville Creek algae, comparing this to N. minutissima and determining an average weight by proportionality. A single value of 3.218 K cal/gm (Trama, 1957) was used to convert algal weights to caloric equivalents.

3) From counts of detrital particles, grouped according to diameter, the total area of detritus in a gut preparation was calculated (i.e. detrital area/field X number of fields/filter). Total detrital area was converted to the weight of that area on the basis of a dry weight of 3.02×10^{-2} mg/mm². This weight value represents an average for leaves of the common species of trees collected from the stream in various stages of decomposition. A caloric value of 5.585 K cal/gm (Trama, 1957) was used to convert animal tissue to caloric equivalents except in cases in which original calorie values were determined (see Table 2, Appendix II; Cummins, 1967; Coffman, 1967).

Since the trophic level approach to the study of energy flow is still the most useful method of ecosystem analysis and since most species do not fall clearly into a single trophic level, a calculation procedure was developed (Cummins et al., 1966) which retains the concept by expressing levels on the basis of tissue support rather than species categories. The technique relies on ingestion trophic data to determine the proportion of each size class of each species to be assigned to one of the three trophic levels (Δ_2 herbivores; Δ_2' or detritivores and Δ_{3-n} or carnivores). Thus, the composite picture that is built up consists of total tissue per unit area of stream bottom supported by the three kinds of calorie intake, i.e. algal, detrital (+ bacteria and fungus) and animal.

THE RIFFLE FAUNA AND FLORA

The riffle fauna of Linesville Creek was found to be quite diverse (Table 1) encompassing 8 phyla representing at least 173 species. The Arthropoda were dominant in

numbers of species, comprising 88%, with 152 species. The class Insecta was the largest arthropod group with 137 or 79% of all species. Seven orders of insects were collected. In decreasing order of number of species they were: Diptera (72), Trichoptera (25), Coleoptera (15), Ephemeroptera (13), Hemiptera (5), Plecoptera (5) and Megaloptera (2). The largest single family was the Chironomidae (Diptera) with 58 species or 42% of the insect species and 34% of the total number of species (Coffman, 1967).

Macrophytic vegetation was not present in the area of Linesville Creek under investigation. In fact, rooted aquatics were practically absent from the entire stream. Filamentous algae, while more common than macrophytic vegetation, was also relatively unimportant in the riffle community. The most important plants were the diatoms of which the species diversity was very great. Those genera found to be ingested by the riffle fauna are shown in Table 2.

RESULTS AND DISCUSSION

Species Diversity and Standing Crop

The diverse nature of the fauna is exemplified by the high indices of diversity shown in Table 3. If each size category is treated as a species, assuming that the size specific nature of trophic habits warrants this, the indices are even higher. (See Appendix I for description of calculations.) The high diversity is to be expected in view of the stability of the trophic structure (see below), the proximity of unglaciated terrain and the merging of three forest types in the area. Particularly diverse were the trichoptera (25 sp.) and the Chironomidae (58 sp). The 28 most common species, on the basis of the number of samples in which they occurred are listed in Table 4.

Standing crop data are presented on a transect basis in Table 5. The values are given both with and without the macropredators (i.e. crayfish and fish) since there is a possibility that the sampling procedures are not adequate to accurately estimate the density of these large, very motile predators. The data have been expressed as numbers; dry weight and calories/m². As can be seen, the standard deviations are quite high when transect averages are presented, reflecting the non-uniform distribution patterns of most species. (Additional detail on standing crop has been summarized in Tables 1 and 2 of Appendix III.) Average Linesville Creek standing crop data have been compared with information on the Firehole River (Armitage, 1961) and Doe Run (Minckley, 1963) in Table 6. Such a comparison indicates that Linesville Creek supports a similar amount of biomass compared to other streams studied, providing substrate type is considered.

The largest number of individuals/m² was found in the Oct. 7, 1964 transect (3A), sample 3 (73,282) and the smallest number was found in the Aug. 2, 1964 transect (1A), sample 1 (1,333). Samples within a transect were remarkably consistent in numbers/m² and generally the differences could be attributed to the natural distribution of the animals in response to the prevailing physical conditions. The general trend was for the smallest number of individuals/m² to be collected along the western margin. It was here that the current was the slowest, the depth the shallowest and the substrate the least riffle-like; all three conditions limiting the distribution of riffle forms. There is also the implication that the non-riffle areas support a smaller qualitative and quantitative standing crop. In addition, at times of low water this area was the first to become exposed. Thus, during the season in which material for this study was collected, the western margin was exposed or subjected to very low water for considerable periods of time. The September 1, 1964 transect (2A) was limited to only four samples since the marginal area was completely exposed. It is interesting to note that transect 2A is one of the most uniform throughout. This may be due to a movement of the marginal fauna toward the central stream area which was reduced in size, thus creating marginal zones with substrate properties of the riffle center, and capable of supporting both marginal and the more rheophilic and lithophilic forms. In all but the Aug. 2, 1964 (1A) and Sept. 1, 1964 (2A) transects, the largest number of individuals/m² was found in one of the center riffle samples. In the case of the

August 2, 1964 (1A) transect, the largest sample was taken on the eastern margin which does not become exposed as readily as the western shore since it is somewhat deeper. In those transects where the largest number of individuals were found in the center of the stream, a number of factors may be involved. Conditions are advantageous in the stream center for riffle forms; the substrate is diverse and, together with the current, provides the necessary factors for the rheophilic and lithophilic fauna. The diversity of the physical system allows for greater biological diversity which in turn itself produces even greater biological diversity through interaction of the components, particularly in terms of predator development. Woodland streams of the temperate zone, being subject to leaf fall, are provided with still another influential factor in distribution. The distribution of organisms through the center riffle area of Linesville Creek seemed to be affected by the accumulation of leaves which attracted numerous primary and detrital consumers as well as the predators associated with them.

Diatom standing crops are reported by sample and transect in Tables 7 and 8 respectively. Because of the clumped nature of diatom distributions, the standard deviation of density estimates are quite high, particularly when data are averaged at the transect level. The intent was to provide a maximum estimate of algal standing crop. Increase in the number of samples would have reduced the estimates somewhat however, the extrapolation from cm^2 to m^2 undoubtedly results in a compensatory underestimate since the substrate suitable for diatom concentration is greater than such an expression would indicate.

Trophic Relationships

The trophic data presented below represent a tremendous effort to provide the most accurate picture possible of the riffle macrofauna ingestion patterns. Table 9 summarizes the per cent of each sample in the fall transects that was gutted. From 13 to 64 % (mean = 31%) of the animals in the 24 samples, constituting the fall collections, were gutted, and when the percentage was low, the absolute numbers were high, reflecting the presence of more animals in the sample. Tables 10 and 11 indicate the level of reproducibility obtained in estimating the trophic relationships of the riffle fauna. The examples illustrate the similarities between replicate counts on the same gut preparation (Table 10) and comparative counts of separate preparations of the same age class of the same species (Table 11).

The data gathered on trophic relationships have been summarized in Table 12, according to percent caloric ingestion, by size classes for five fall transects taken in 1964 and 1965. The fauna was dominated by algal feeders and predators, but large amounts of detritus were consumed, not through the presence of numerous species feeding predominantly on detritus, but by virtually every species consuming at least some detrital food.

Variation in the diet of natural populations, even within a given size class, is to be expected; in the present study very little variation was found in the populations of algal, detrital and algal-detrital feeders, however, the predators exhibited significant variation in prey consumption (details of predator-prey relationships are given in Appendix IV). In this study, the variation in diet was reduced within species and size classes of those species by calculating an ingestion value per individual (Fig. 3). This value incorporated data from all the animals examined and was used for each individual in the population as a measure of the quality and quantity of food used in the trophic calculations for that particular size class and species.

Three kinds of food were important in the riffle area for which data are presented here. The algal food in the fall community was almost completely diatoms with a few filamentous algae, particularly *Cladophora* spp. The amount of non-diatom algae was much greater at other times of the year, particularly in the spring. The detrital part of the food consisted primarily of deteriorated plant and animal material with their associated bacterial and fungal flora. Depending on the state of the detritus, vascular plant tissue and fungal hyphae and spores could be readily identified. The animal food consisted primarily of insects, but some protozoans, annelids and nematodes were also observed.

The gut contents of each size class were examined for the three food categories and

the number of items of each kind as well as weight and calorie equivalents were calculated (Fig. 3). The per cent contributions of each of the three food categories (diatom, detritus, animal) were calculated for the total number, total weight and total calories of food ingested. The results of multiplying the standing crop in numbers, weight and calories per unit area of a size class of a particular species by the appropriate per cent ingestion of the same three parameters, numbers, weight and calories of items ingested, provided three sets of data to use in placing that size class in one or more trophic levels.

In order to minimize the effects of the unusual distributional characteristics of the crayfish and fish, their impact has been spread evenly over the samples. (This has a similar effect as their removal from the calculations but seems to provide a more realistic estimate than results when they are included only with the samples in which they were collected.) The consistency (that is stability) in the relative amounts of tissue supported in each of the three "trophic channels" is apparent in Table 13. The per cent tissue support averaged about 20% for Λ_2 (algal ingestion), 5% for Λ_2' (detrital ingestion) and 75% for Λ_{3-n} (animal ingestion).

Based on trophic and standing crop data the impact of the macroconsumers on their food supplies, assuming various turnover rates, and assimilation rates have been estimated and are presented in Tables 13 through 16. The calories of primary production (Λ_1) ingested are expressed on an instantaneous basis (that is the amount actually measured in the guts of the sampled animals), times 24 and times 48 (Table 13). The latter two estimates of ingestion are based on two rates of passage through the gut. The first assumes that the amount of material in the gut is processed each hour, and the second sets the rate of processing at once every half hour. The actual rates undoubtedly vary with the species. Brown (1961) found that detritus was kept in the gut for a shorter period of time than algae, however, most of the Linesville Creek species ingested both materials, and the rate of passage for the two kinds of food should have been the same. The instantaneous and x 48 values of ingestion per day for the primary consumers (Λ_2 or algal, Λ_2' or detrital) represent what are thought to be the minimum and maximum values for the system. The ingested calories of animals by the carnivore levels Λ_{3-n} are expressed on an instantaneous basis and x 12. Predators tend to feed more periodically than the primary consumers, and the material is held in the gut for a longer period of time. A maximum value for the Linesville Creek predators was thought to be represented by a two hour period of feeding and processing, repeated 12 times a day. The standing crop and ingestion of the predators (Λ_{3-n}) are expressed with the standing crop and the ingestion of the macro-predators (*Cottus bairdii*, *Orconectes obscurus*, *Cambarus robustus*) included and excluded. The absolute number of standing crop calories and ingestion calories in each of the categories varied between transects. The per cents impact on the food calories (Λ_1 , Λ_1' , $\Lambda_2 + \Lambda_2'$, that is algae, detritus and prey) made by the consumers ($\Lambda_2, \Lambda_2', \Lambda_{3-n}$) are shown in Table 13. In general, the impact on the diatom standing crops was only slight when the total amount of the instantaneous ingestion was considered. However, the x 24 and x 48 ingestion values range from 1.18% to 72.85% of the standing crop consumed per day. The extremely high value occurred in transect 2B which had the most ingestion of diatom calories but the second smallest standing crop. A daily impact of 73% on the diatom caloric standing crop is inconceivable, in spite of a rapid turnover of the diatom biomass and it is probable that the diatom standing crop in transect 2B was underestimated. The great amount of diatom ingestion was carried out by *Psilotreta indecisa*, *Coera calcarata* and to a lesser extent by *Glossosoma nigrum* and *Psephenus herricki*. The standing crop values for diatoms represent an extrapolation to a per square meter basis. However, as Scott (1960) has shown for certain kinds of substrate, particularly riffle substrates, the total surface area may be considerably larger. If this is the case, then all of the per cents of impact would be lowered accordingly. The detritus standing crop in calories/m² was at its largest in the two October transects. The per cent impact in the detritus standing crop was typically under 10%, even at a maximum estimate. One transect, 1B, provides an impact of 187% on the detritus standing crop. However, the detritus turnover in the stream may be very rapid. One of the most striking features of the data shown in Tables 14-16 is the tremendous impact of the predators on the other animals. When

the numbers of calories of the macropredators assigned to support by diatom and detritus calories are included in the standing crop transect averages for Λ_2 and Λ_2' and the ingestion of the macropredators is included in the transfer categories, then the per cent impact of the predators ranges from 1.58% to 9.64% on an instantaneous basis (Table 14). If this is extended to a daily impact, estimating the gut is filled every two hours, then the per cent impact ranges between 18.98% and 115.63%. The addition of the macropredators to the trophic-energetic balance for the $5/m^2$ of each transect may add too much ingestion for that small area. It is suggested that the macropredators may require a considerable amount of area to be in trophic harmony with the system. When the macropredator standing crop and ingestion are removed, the instantaneous impact of the predators on the primary consumers is lowered and much more uniform, with a range from 2.22% to 5.88%; the range is 36.19% to 70.50% for a daily impact estimate (12 times the instantaneous impact). It is obvious that these impact values would, at best, provide material for about 20 days, and 20 days has usually been considered too short of a time to replenish the entire stream primary consumers in terms of population numbers. However, 20 days might be a reasonable figure in terms of biomass turnover.

Several factors may have produced the high per cent impact values of the predators on the primary consumers. The amount of predation for some species, such as the hydropsychids, may have been overestimated, since these species retain head capsules and other sclerotized parts in the proventriculus. These parts are held there and broken up and eventually passed through the gut. On the other hand, the role of fluid-feeders may have been underestimated. Errors were probably more significant in the measurements of the prey. The estimates of standing crop were more accurate in including the larger animals, however, the majority of the predators feed on the smaller species and size classes. Thus, the amount of available calories may have been underestimated. Waters (1962) has suggested another possibility. He contends that the animals consumed by predators are those that never find a physical location into which they fit biologically. Thus, these animals that make up a considerable portion of the drift do not show up in the standing crop figures. Anderson (1967) has shown that 5,000 trichopterans/ m^2 are involved in drift/day, whereas only 7,500 trichopterans/ m^2 were found in the standing crop. Another problem arises from the consideration of the nutritional requirements of the predators. The predator biomass, even with the macropredators removed, was quite large. If it can be assumed that the growth of predators/day is negligible and that the respiration of the animal tissue consumes about 70% of the assimilated calories/unit time, then the daily energy intake must at least be equal to the daily output of respiration.

Assimilation rates for each macroconsumer level ($\Lambda_{3-n}, \Lambda_2 + \Lambda_2', \Lambda_2, \Lambda_2'$) based on 30 day or 7 day turnover times (assumed to represent the upper and lower limits) for the standing crop are shown in Table 15. The caloric standing crop of each level is given. Turnover/day was calculated by dividing the standing crop by 30 and 7. Assuming that the turnover/day is growth and should be about 30% of the assimilated calories/day, then the respiration/day would be 70% relative to the turnover (growth/day). The total assimilation/day would be the sum of the turnover (growth/day (30%) and the respiration/day (70%) (all the values in Table 14 are per square meter). In all five transects, the assimilation/ m^2 /day of the secondary macroconsumers (Λ_{3-n}) was less than the primary consumer of algae (Λ_2) but greater than assimilation/ m^2 /day of the primary consumers of detritus (Λ_2'). In general, the values were quite consistent. The differences in the quantity of calories assimilated reflect the differences in standing crop. Feeding rates for each of the levels have been calculated and are shown in Table 15. The feeding rates relate to hypothetical animals rather than real animals. As a result, the feeding rates reflect, in part, the general feeding rate for all of the animals collected. If, for instance, a number of animals in a transect were of large size, ingested many more calories of food than smaller animals and took longer to process them, then the feeding rate would tend to shift toward slower values. Transect 2B has feeding rates for $\Lambda_2 + \Lambda_2'$ and Λ_2 that are much higher than any of the other transects. The caloric ingestion/individual was also the greatest of any of the other transect values. The feeding rates were calculated from the assumption that only 40% of the ingested calories were assimilated, the others being egested. The calories ascribed to instantaneous assimilation must be processed often enough per unit time to

equal the expense of respiration and growth. The gut turnover/day in Table 16 represents "instantaneous assimilations" required per day for each of the levels. These values were calculated by dividing the calories of assimilation/m²/day (assuming either a 30 or 7 day turnover) by the instantaneous assimilation/m²/day. The gut turnover time in days is also expressed in Table 16 as the feeding period in hours. The calculated feeding periods for the Λ_{3-n} levels were reasonable. They ranged between 4.1 and 20.0 hours when a turnover period of 30 days was used and between 0.9 and 4.9 hours when a turnover period of 7 days was used. The feeding periods for the primary consumer levels were generally quite long. Most of the data on the feeding rates of aquatic insects, in particular, indicate rates near 30 minutes. Table 16 also shows the calculated total ingestion/m²/day, based on either 30 day or 7 day turnovers of the standing crop. The number of days required by Λ_{3-n} to deplete the standing crop of their prey ($\Lambda_2 + \Lambda_2'$) was calculated by dividing the standing crop of the primary consumers ($\Lambda_2 + \Lambda_2'$) by the ingestion/m²/day. When a 30 day turnover time for the Λ_{3-n} standing crop was assumed, the calculated turnover time of the primary consumers was between one and two weeks. A turnover time of 7 days required that the $\Lambda_2 + \Lambda_2'$ standing crop turn over about every one to three days. Table 17 contains some calculated rates of assimilation of the combined macroconsumer levels ($\Lambda_{3-n} + \Lambda_2 + \Lambda_2'$). The data are expressed as Kcal/m² and were calculated for assumed turnover times of 30 and 7 days, on assimilation efficiency of 40% and a growth efficiency of 30%.

A number of factors concerning the static aspects of the community structure and the more dynamic trophic relationships of the community, when examined together, illustrate for the Linesville Creek riffle system a rather rigid framework within which the biological processes take place. This framework maintains the essential criteria by which we recognize the riffle system. Variation is built into the system; indeed, a capacity for variations in the riffle system is necessary, since it is only through the "proper" response to physical changes in terms of biological variation that the system we recognize as a typical riffle biotope has survived. This capacity for the "proper" response is found in the species composition, species diversity age structure, standing crop and trophic relations. The ecological system that is capable of responsive variation, in these and other respects, is capable of maintaining its identity, providing the physical environment does not prohibit it. This ability is often referred to as stability. In this regard, the Linesville Creek riffle system was found to be very stable in that, in spite of variation seen in species composition and standing crop, the relative relationships of the trophic structure, viewed at the level of tissue support rather than individual species populations, exhibited great consistency.

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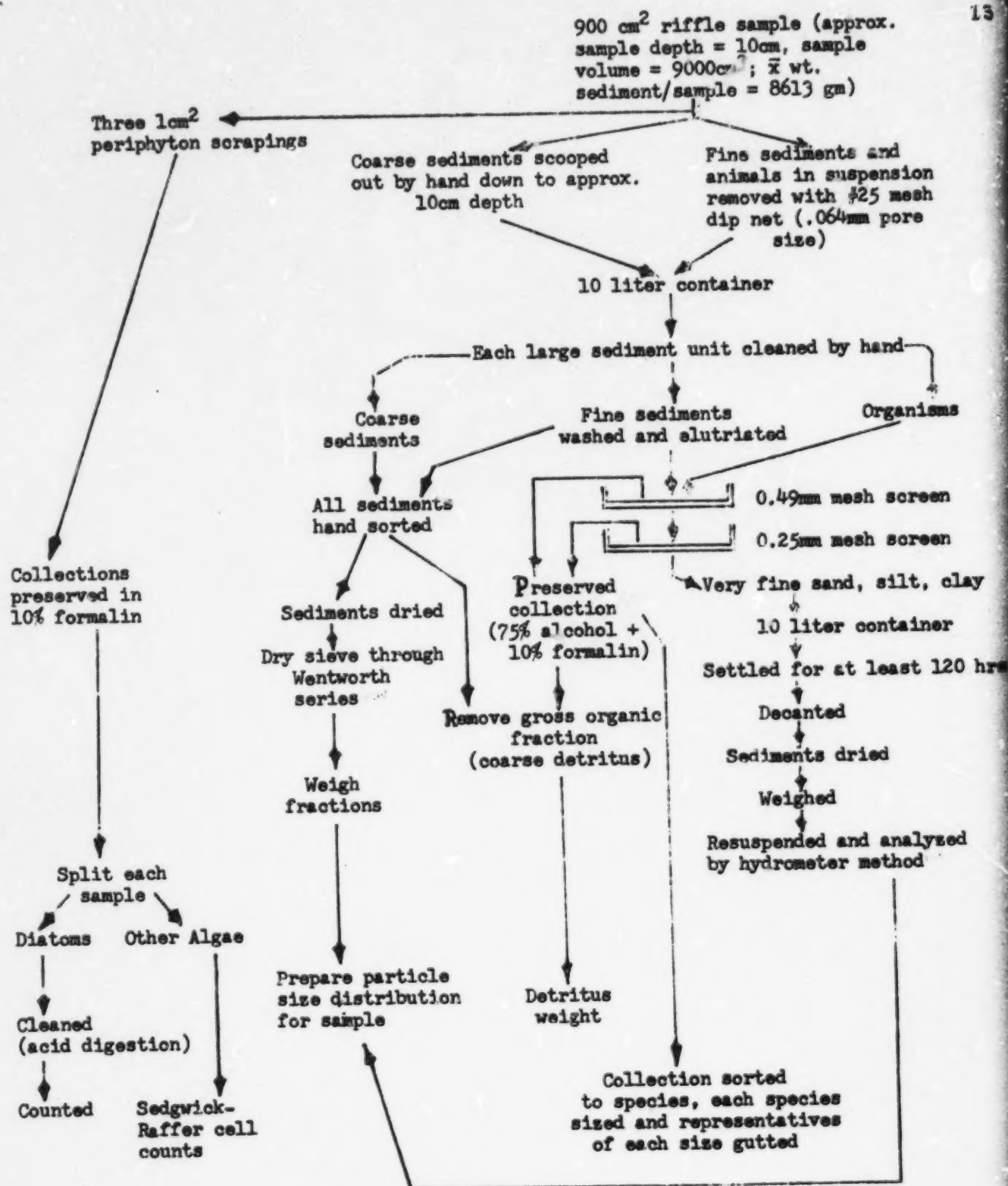


Fig. 1. Methods of field sampling and laboratory processing.

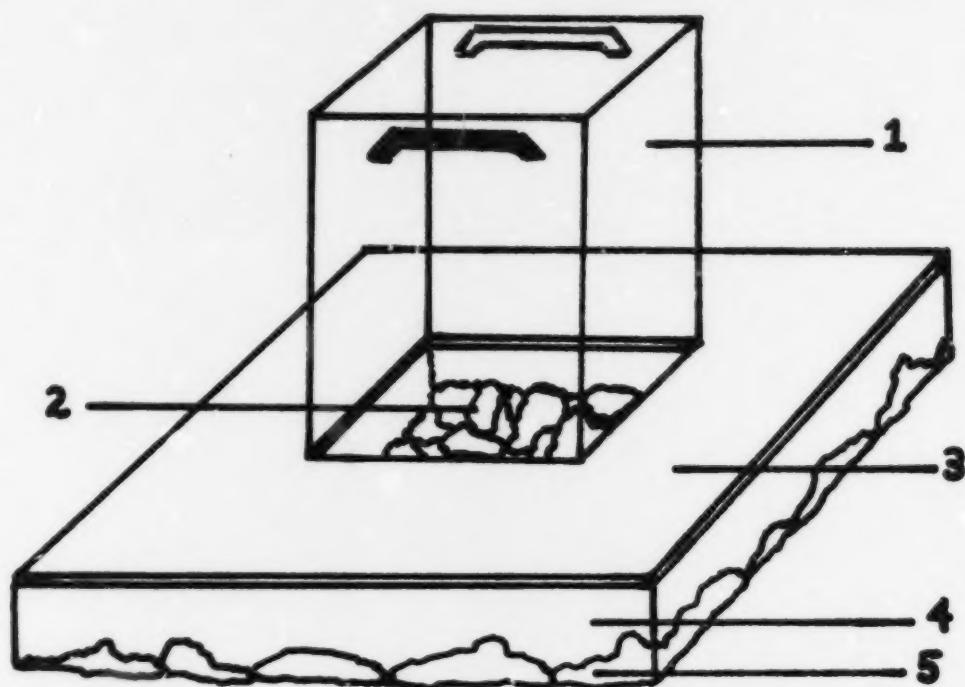


Figure 2. Riffle benthos sampling device: (1) water tight upright section (plexiglass) with carrying handles, (2) substrate seen within sample area (total sample area 900 cm²), (3) plexiglass base (investigators stand or kneel on this base during sampling), (4) sponge rubber base (10 cm thick) shown compressed around substrate particles as it is during sampling, (5) substrate as seen from outside edge of sampler.

Ingestion by size class and species

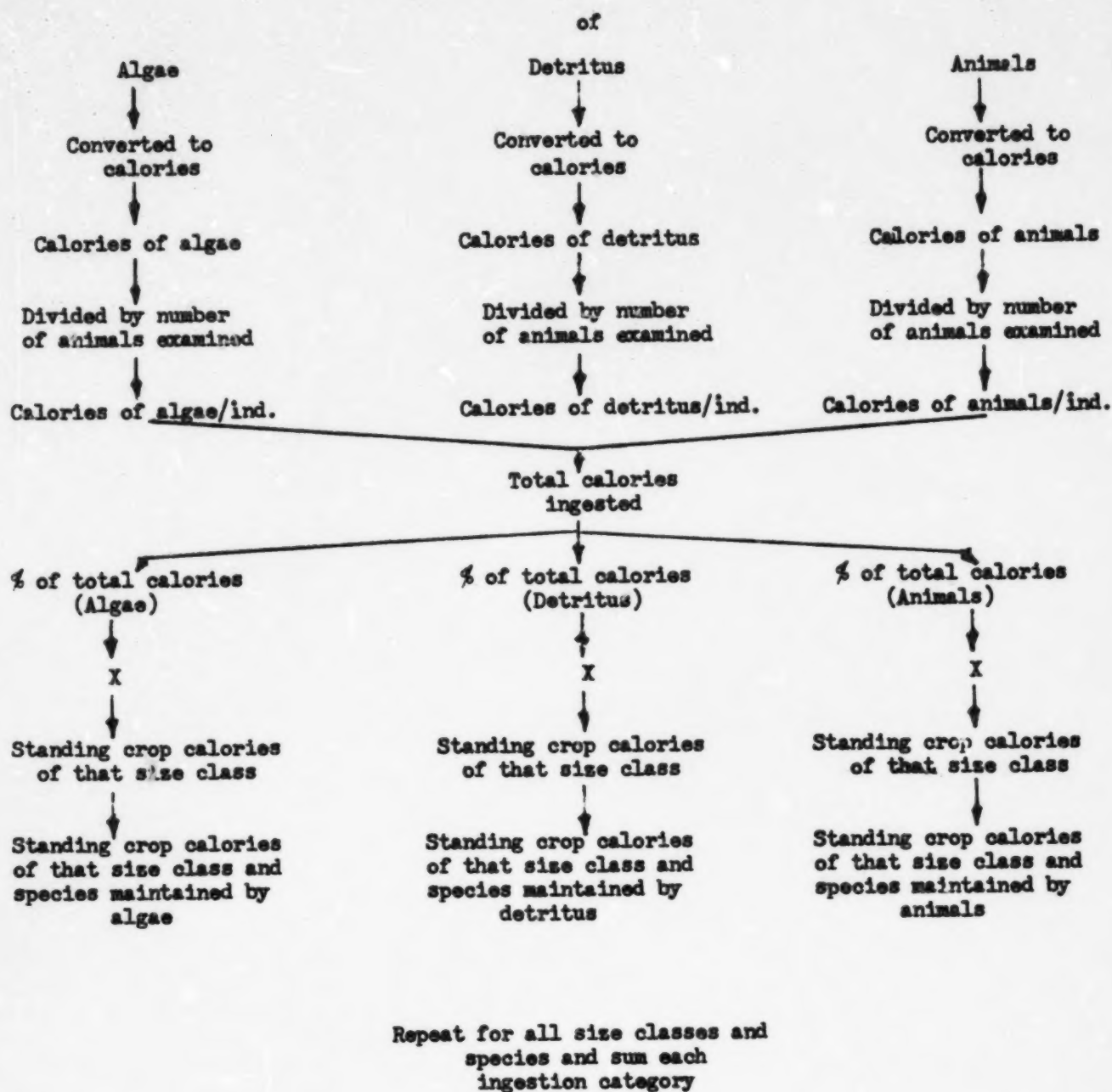


Fig. 3. Determination of "tissue support" trophic structure

Table 1. The riffle fauna of Linesville Creek (Wallace Woods), Crawford County, Pennsylvania. (Numbers in parentheses are the suggested number of species within that taxon.)¹

Annelida (6)

Hirudinea (1)

Oligochaeta (5)

Branchiobdellidae (1)

Naididae (2)

Allonais paragnayensis

Nais behningi Michaelsen

Tubificidae (2)

Limnodrilus hoffmeisteri Claparede

Rhyacodrilus montanus

Arthropoda (152)

Arachnida (about 12)

Hydracarina (about 12)

Crustacea (3)

Copepoda (1)

Harpacticoida (1)

Decapoda (2)

Cambarus robustus Girard

Orconectes obscurus (Hagen)

Insecta (137)

Coleoptera (15)

Dryopidae (2)

Helichus sp. 1 Erichson

H. sp. 2²

Dytiscidae (2)

Hydroporus undulatus Say²

H. sp. 1

Elmidae (4)

Dubiraphia sp. 1 Sanderson

Limnius laticulus Le Conte

Optioservus sp. 1 Sanderson

Stenelmis beameri (Sanderson)

Macronychus sp. Miller

Hydrophilidae (5)

Helocombus bifidus Le Conte²

Helophorus lineatus Say²

Laccobius sp. 1 Erichson

Paracymus sp. 1 Thomson

Troniatermus glaber (Berbst)

Psephenidae (2)

Ectoparia sp. 1 Le Conte

Psephenus herricki (De Kay)

Diptera (72)

Ceratopogonidae (2)

Palpomyia sp. 1 Meigen

Bessia sp. 1 (Johannsen)

Chironomidae (Tendipedidae) (58)

Chironominae (Tendipedinae) (24)

Chironomini (Tendipedinae) (15)

Cryptochironomus vulneratus Zetterstedt

¹ The higher level taxonomy follows the basic outline of Ward and Whipple (1959)

² Not found in quantitative samples

³ From Roback (1957)

⁴ From Johannsen (1937)

⁵ From Ross (1944)

- C. sp. A Kieffer
C. sp. B
C. s. l. sp. B (Johannsen)
C. sp. 3⁴
Limnochironomus modestus (Say)
Microtandipes pedellus (DeGeer)
Paratandipes albimanus Meigen
Phaenopsectra (Tribelos) jucundus (Walker)
P. (Tanytarsus) obediens (Johannsen)
Polypedilum fallax group sp.
P. sp. nr. sordens (Van der Wulp)
P. scalaenum (Schränk)
Stictochironomus sp. 2 Kieffer³
Xenochironomus sp. nr. scopula
 Tanytarsini (Calopsectrini) (9)
Tanytarsus conversus (Johannsen)
T. exiguus (Johannsen)
T. sp. nr. exiguus
T. sp. nr. polita (Malloch)
T. sp. 3 Van der Wulp³
T. sp. 4³
T. sp. 5³
Stempellina sp. nr. johannseni (Bause)
Zaurelia sp. nr. pentatoma (Kieffer)
 Diamesinae (3)
Diamesa nivoriunda (Fitch)
Potthastia longimanus Kieffer
Prodiamesa sp. nr. bathyphila (Kieffer)²
 Orthocladiinae (Hydrobaeninae) (23)
Brillia flavifrons (Johannsen)
Corynoneura taris Roback
C. sp. 1 Winertz³
 Genus nr. Corynoneura sp. 1
Cricotopus sp. nr. bicinctus (Neigen)²
C. sp. nr. exilis Johannsen
C. sp. nr. junus Roback
C. sp. nr. nostocicola or fuscatus (Wirth)²
Diplocladius cultriger (Kieffer)
Eukiefferiella sp. nr. brevinervis (Malloch)
E. sp. nr. longicalcar (Kieffer)
E. sp. nr. sordens (Johannsen)
E. sp. 2 Thienemann
 Genus nr. Eukiefferiella sp. 1
Hydrobaenus sp. nr. dubitatus Johannsen²
H. nivoriundus (Johannsen)
H. sp. nr. paradoreus Roback
 Genus nr. Metriocnemus sp. 1
Psectrocladius sp. nr. 4 Kieffer³
Smittia sp. nr. E Holmegren
Trichocladus sp. 3 Kieffer
 Unknown Trichocladus or Smittia sp.
 Unknown Orthocladiinae sp.
 Tanypodinae (Pelopiinae) (8)
Anatopynia sp. nr. fatuosa (Johannsen)
Pentaneura auriensis Roback
P. carnea group sp.
P. melanops group sp.
P. pilosella (Loew)
P. sp. A
P. sp. B
Procladius adumbratus Johannsen

- Dixidae (1)
Paradixa sp. 1 Tonnoir²
- Epididae (1)
Hemerodromia sp. 1 Meigen
- Psychodidae (2)
Pericoma sp. 1 Walker²
Psychoda alternata Say
- Rhagionidae (1)
Atherix variegata Meigen
- Simuliidae (2)
Prosimulium m'xtum Syme and Davies
Simulium venustum Say
- Tabanidae (1)
Tabanus sp. 1 Linnaeus sens. lat.
- Tipulidae (5)
Antocha sp. 1 Osten Sacken
Dicranota sp. 1 Zetterstedt
Eriocera fultonensis Alexander
Erioptera spp. Meigen²
Tipula spp. Linnaeus
- Ephemeroptera (13)
- Baetidae (2)
Centroptilum album (McDunnough)
Pseudocloeon sp. 1 Klapalek
- Caenidae (1)
Caenis anceps Traver
- Ephemeridae (2)
Ephmera simulans Walker
E. varia Eaton
- Ephemerellidae (2)
Ephemerella aestiva McDunnough
E. dorothea Needham
- Heptageniidae (3)
Stenonema canadense Walker
S. fuscum Clemens
S. tripunctatum (Banks)
- Leptophlebiidae (2)
Choroterpes sp. 1 Eaton
Habrophlebia des americana Banks
- Siphonuridae (1)
Isonychia albomanicata Needham
- Hemiptera
- Belastomatidae (1)
Belastoma sp. 1 Latreille
- Gerridae (1)
Gerris remigis (Say)²
- Nepidae (1)
Ranatra fusca Palsot de Beauvois
- Veliidae (2)
Microvelia americana (Uhler)
Rhagovelia choreutes Hussey²
- Megaloptera (2)
Nigrinia serricornis (Say)
Sialis sp. 1 Latreille
- Plecoptera (5)
- Chloroperlidae (1)
Chloroperla sp. 1 Newman
- Nemouridae (2)
Nemoura venosa Banks
Taeniopteryx maura Pictet

Perlidae (2)

Acroneturia lycorias (Newman)
Phasganophora capitata Pictet

Trichoptera (25)

Goeridae (1)

Goera calcarata Banks

Glossosomatidae (1)

Glossosoma nigrior Banks

Helicopsyichidae (1)

Helicopsyche borealis Hagen

Hydropsychidae (6)

Cheumatopsyche aphantha Ross

C. oxa Ross

Hydropsyche betteni Ross

H. bronta Ross

H. glossinae Banks

Unknown Hydropsychid sp.

Hydroptilidae (2)

Hydroptila consimilis Morton

Unknown Hydroptilid sp.

Lepidostomatidae (1)

Lepidostoma sp. 1 Rambur²

Leptoceridae (2)

Athripsodes sp. a Billberg⁵

Triaenodes sp. 1 McLachlan

Limnephilidae (5)

Neophylax nacatus Denning

Platycentropus sp. 1 Ulmer²

Pycnopsyche antica (Walker)

P. guttifer (Walker)²

P. lepida (Hagen)²

Odontoceridae (1)

Psilotreta indecisa (Walker)

Philopotamidae (1)

Chimarra aterrima Hagen

Phryganeidae (1)

Ptilostomis semifasciata (Say)

Psychomyiidae (3)

Nyctiophylax sp. A (Flint)

Polycentropus confusus Hagen

P. cinereus Ross

Psychomyia flavida Hagen

Aschelminthes (2?)

Nematoda (1?)

Rotifera (1?)

Coelenterata (1)

Hydrozoa (1)

Hydrida (1)

Hydra sp.

Mollusca (4)

Gastropoda (3)

Ferrissia rivularis Say

Physa sp. 1 Draparnaud

Gyraulus sp. 1 Charpentier

Pelecypoda

Sphaerium sp. 1 Scopoli

Pisidium sp. 1 Say

Platyhelminthes (1)
 Turbellaria (1)
 Tricladida (1)

Dugesia sp. 1 Girard

Porifera (1)
 Demospongiae (1)
 Haplosclerina (1)
 Spongillidae (1)

Chordata (6)
 Vertebrata (6)
 Osteichthyes (6)

Cottus bairdii Girard
 Sculpin
Eucalia inconstans (Kirtland)
 Brook Stickleback
Etheostoma bleennioides Rafinesque
 Greenside Darter
E. caeruleum Storer
 Rainbow Darter
E. flabellare Rafinesque
 Fantail Darter
E. nigrum Rafinesque
 Johnny Darter
E. exile (Girard)
 Iowa Darter

Table 2. The diatom genera found to be ingested by the Linesville Creek riffle fauna.

<u>Achnanthes</u>	<u>Diploneis</u>	<u>Navicula</u>
<u>Amphipleura</u>	<u>Epithemia</u>	<u>Nedum</u>
<u>Amphora</u>	<u>Eunotia</u>	<u>Nitzschia</u>
<u>Coloneis</u>	<u>Fragilaria</u>	<u>Pinnularia</u>
<u>Cocconeis</u>	<u>Frustulia</u>	<u>Pleurosigma</u>
<u>Cyclotella</u>	<u>Gomphonema</u>	<u>Rhoicosphenia</u>
<u>Cymatopleura</u>	<u>Gyrosigma</u>	<u>Stauroneis</u>
<u>Cymbella</u>	<u>Melosira</u>	<u>Surirella</u>
<u>Diatoma</u>	<u>Meridion</u>	<u>Synedra</u>

Table 3. Mean estimates of community diversity and diversity/individual for each transect. P = Patten, 1962; M = Margalef, 1951). Values are bits/ 900 cm².

Transect	No. of species	Species		Comm. div. (M)	No. size classes	Size classes treated as species		
		Comm. div. (P)	Div./Ind. (P)			Comm. div. (P)	Div/ ind. (P)	Comm. div. (M)
1A	39	746.09	1.81	6.62	73	926.08	3.58	12.23
2A	39	675.83	1.85	6.49	77	1,378.17	3.76	12.81
3A	53	3,741.30	1.50	7.50	110	6,238.02	3.72	15.52
1B	67	4,537.56	1.51	8.24	150	10,973.37	3.62	18.57
2B	63	2,649.69	1.44	8.24	149	7,395.26	3.97	19.73

Table 4. The dominant Linesville Creek riffle taxa based on the frequency of occurrence, the total number of individuals and the size of the biomass. The macropredators have been excluded.

Taxon	No. of Samples	Taxon	No. of Samples
<u>Antocha</u> sp.	24	<u>Polycentropus confusus</u>	21
<u>Optioservus</u> sp.	24	<u>Polypedilum scalaenum</u>	21
<u>Pentaneura melanops</u>		<u>Stenelmis beameri</u>	21
group sp.	24	<u>Tanytarsus exigua</u>	21
<u>Psephenus herricki</u>	24	<u>Atherix variegata</u>	20
<u>Helicopsyche borealis</u>	23	<u>Centroptilum album</u>	20
<u>Psychomyia flavida</u>	23	<u>Eukiefferiella</u> sp. 2	20
<u>Corynoneura</u> sp.	22	<u>Hydropsyche bronta</u>	20
<u>Habrophlebiodes americana</u>	22	<u>Hydropsyche slossonae</u>	20
<u>Microtendipes pedellus</u>	22	<u>Tanytarsus</u> sp. nr. <u>polita</u>	20
<u>Oligochaete</u> spp.	22	Gen. nr. <u>Eukiefferiella</u> sp.	19
<u>Glossosoma nigrior</u>	21	<u>Hemerodromia</u> sp.	19
<u>Cheumatopsyche</u> sp.	21	Gen. nr. <u>Metriocnemus</u> sp.	19
<u>Cricotopus exilis</u>	21	<u>Psilotreta indecisa</u>	19
<u>Palpomyia</u> sp.	21	<u>Stenonema tripunctatus</u>	19

Table 5. Mean transect standing crop values with and without the macropredators *Cambarus robustus*, *Orconectes obscurus* and *Cottus bairdii*. (Transect dates: 1B, Aug. 2, 1964; Sept. 1, 1964, Oct. 7, 1964; Aug 4, 1965; Oct 2, 1965.)

Transect	no. / m ²	With macropredators		Without macropredators	
		mg./m ²	cal./m ²	no/m ²	cal./m ²
1A	4,853±4,067*	18,154±17,627	69,753±68,872	4,846±4,063	2,360±1,399
2A	4,091±603	7,690±12,206	33,607±49,464	4,088±598	1,285 ± 844
3A	20,751±29,506	15,102±21,205	62,657±71,628	20,749±29,473	6,247±3,214
1B	33,746±6,310	101,472±90,868	379,684±349,371	33,721±6,327	6,359±1,179
2B	20,702±3,382	25,229±37,046	108,902±147,560	20,693±3,380	6,626±1,382
					36,662±7,535

* Standard deviation

Table 6. Standing crop values for Linesville Creek and two other streams. The Firehole River (Armitage, 1961) and Doe Run (Minckley, 1963) data indicate the necessity of considering the physical and biological factors of the sampling site.

Stream	Substrate or area	No. of samples	Original samp. size	No/ m ²	Mg/m ²	Cal/m ²
Firehole River	rubble	37	ft. 2	1,230	10,003	
"	bedrock	56	"	852	4,032	
Doe Run	Fissidens bed	15	"	93,945	312,775	
"	main channel		"	101,314	117,829	
"	moss bed		"	1,581	404	
"	marl riffles	12	"	1,591	1,482	
"	riffles lateral to channel	15	"	2,878	3,782	
"	unvegetated riffle sta. II		"	5,504	7,708	
"	riffles lateral to marl		"	1,624	2,169	
"	<u>Nasturtium</u> beds		"	9,734	17,233	
"	<u>Myriophyllum</u> beds		"	37,311	30,738	
"	silt covered eddy		"	4,556	6,998	
"	shifting sand		"	1,995	1,853	
"	large pools		"	6,060	5,374	
Linesville Creek	rubble	24	900 cm ²	17,845	4,829	26,549
"	rubble	24	"	17,359	34,606	143,132

*These values do not include the decapod and fish standing crop.

Table 7. The mean standing crop of diatoms in each sample as number of cells/ m², dry weight in grams/ m² and kilocalories / m².

Transect	Sample	No. of subsamples	Cells/ m ² x 10 ⁸	Grams/ m ²	K cal/ m ²
1A	1	3	696 ± 219*	505 ± 168	1,626 ± 540
1A	2	2	677 ± 92	565 ± 95	1,816 ± 303
1A	3	3	513 ± 153	428 ± 131	1,376 ± 423
1A	4	3	1,257 ± 730	1,049 ± 609	3,375 ± 1,960
1A	5	1	342	285	918
2A	1	3	154 ± 61	129 ± 51	414 ± 165
2A	2	3	294 ± 148	245 ± 124	788 ± 400
2A	3	3	303 ± 149	252 ± 125	812 ± 327
2A	4	3	19 ± 9	16 ± 7	52 ± 23
3A	1	3	41 ± 8	34 ± 7	109 ± 22
3A	2	3	7 ± 2	6 ± 1	21 ± 3
3A	3	3	103 ± 123	86 ± 103	277 ± 329
3A	4	3	128 ± 170	107 ± 141	344 ± 456
3A	5	3	3 ± 2	2 ± 1	7 ± 4
1B	1	3	12 ± 6	9 ± 5	30 ± 18
1B	2	3	194 ± 92	162 ± 76	521 ± 246
1B	3	3	427 ± 160	356 ± 134	1,145 ± 430
1B	4	3	153 ± 69	128 ± 58	582 ± 186
1B	5	2	81 ± 12	68 ± 10	217 ± 31
2B	1	2	94 ± 16	78 ± 13	251 ± 41
2B	2	3	106 ± 11	89 ± 9	284 ± 29
2B	3	3	215 ± 211	179 ± 173	576 ± 558
2B	4	3	35 ± 11	29 ± 10	94 ± 30
2B	5	2	7 ± 1	6 ± 1	119 ± 3

Table 8. The mean standing crop of diatoms for each transect as number of cells/ m², dry weight in grams/ m² and kilocalories/ m².

Transect	Total no. of subsamples	Cells/ m ² x 10 ⁸	Grams/ m ²	K cal/ m ²
1A	12	679 ± 310	566 ± 259	1,822 ± 833
2A	12	193 ± 116	161 ± 97	517 ± 311
3A	15	56 ± 51	47 ± 42	152 ± 136
1B	14	173 ± 141	145 ± 118	465 ± 379
2B	13	91 ± 72	76 ± 60	249 ± 192

* Standard deviation

Table 9. A comparison of the number of animals in each sample and the number of animals actually examined for gut contents.

Transect	Sample	Total no. of animals	No. exam.	No. exam. as percent of total
1A Aug. 2, 1964	1	118	73	62
	2	215	126	59
	3	197	83	42
	4	684	372	54
	5	948	369	39
2A Sept. 1, 1964	1	431	229	53
	2	315	175	56
	3	387	211	54
	4	336	197	59
3A Oct. 7, 1964	1	446	200	45
	2	827	296	36
	3	6596	838	13
	4	982	327	33
	5	488	191	39
1B Aug. 4, 1965	1	2750	750	27
	2	2206	600	27
	3	3163	828	26
	4	3600	869	24
	5	3467	777	22
2B Oct. 2, 1965	1	1404	906	64
	2	2243	1106	49
	3	1904	715	37
	4	1964	811	41
	5	1802	619	34
TOTALS		37473	11668	31
MEAN / SAMPLE		1561	486	31

Table 10. Replicate counts made on a filter (No. 13-2-30) prepared from five size class two Helicopsyche borealis larvae. Complete scanning of the material yielded no animal fragments. The mean number of diatoms and detrital units are given with their standard deviations.

Diatom genera	Total count in 10.7 linear mm. under oil immersion (1,500 x)			Diameter of detrital particles (mm units)	Counts converted to number of standard diameter (0.5 mm units) detrital particles		
	First count	Second count	Third count		First count	Second count	Third count
Achnanthes	151	213	136	0.5	49	45	46
Cocconeis	31	40	36	1.0	26	24	18
Cymbella	31	23	22	1.5	6	9	9
Amphora	25	17	17	2.0	8	12	12
Navicula	19	19	15	2.5	5	10	0
Nitzschia	16	17	9	3.0	6	0	0
Undet. (diatoms)	15	12	14				
Fragilaria	13	9	5				
Gomphonema	2	4	0				
Eunotia	1	0	0				
TOTALS	304	354	254		100	100	85
Mean	304 ± 50			Mean	95 ± 12		

Table 11. Comparison of four measurements of the ingestion by size class five *Microtendipes pedellus*. Each of the four filters were made from the guts of three larvae. The mean number of diatoms and detrital units are given with their standard deviations.

Diatom Genera	Total count per linear mm* (oil immersion; 1,500 x)				Detrital particle size	Total count of standard detrital particles (i.e., diameter 0.5 micrometer units) at 400 x			
	First filter	Second filter	Third filter	Fourth filter		First filter	Second filter	Third filter	Fourth filter
<i>Achnanthes</i>	35.7	33.3	39.6	33.0	0.5	75	89	95	100
<i>Navicula</i>	6.8	3.9	6.9	3.4	1.0	82	62	70	40
<i>Cymbella</i>	4.5	3.3	4.4	2.1	1.5	30	30	33	27
<i>Nitzschia</i>	4.1	3.6	4.4	3.9	2.0	44	48	32	60
<i>Ampora</i>	2.0	0.7	0.2	0.1	2.5	35	25	15	25
<i>Cocconeis</i>	1.1	1.2	1.2	0.1	3.0	72	60	42	18
<i>Fragilaria</i>	0.9	0.6	0.8	0.1	3.5	56	7	0	42
<i>Comphonema</i>	0.7	0.4	0.4	1.1	4.0	48	56	24	0
<i>Cyclotella</i>	0.4	2.2	0.2	0.4	4.5	27	45	9	0
<i>Synedra</i>	0.4	0.3	0.4	0.1	5.0	20	20	20	30
<i>Diatoms</i>	0.2	0.0	0.0	0.1	5.5	22	11	0	11
<i>Melosira</i>	0.2	0.1	0.4	0.9	6.0	0	12	12	12
<i>Surirella</i>	0.2	0.0	0.0	0.1	6.5	0	0	13	0
<i>Diploneis</i>	0.0	0.1	0.0	0.0	7.0	28	14	42	0
<i>Frustrula</i>	0.0	0.1	0.0	0.0	7.5	15	0	0	0
<i>Cymatopleura</i>	0.0	0.0	0.2	0.0	8.0	16	0	16	0
<i>Cyrosigma</i>	0.0	0.0	0.2	0.0					
<i>Meridion</i>	0.0	0.0	0.2	0.0					
Undetermined	3.4	3.3	4.0	1.4					
Totals	60.4	53.3	63.5	47.1	Totals	571	479	423	365
Mean	56.0 $\pm$ 7.4				Mean	460 $\pm$ 88			

* Since different total linear mm were read on each filter, the counts have been converted to the common standard of cell/linear mm.

Table 12. Relative percent ingestion as calories of algae, detritus and animals. Per cents based on all records by size class and for the taxon as a whole. Transects (Composed of five samples each, except four for 2A) from which data were taken are as follows: 1A = 8/2/64; 2A = 9/1/64; 3A = 10/7/64, 1B = 8/4/65; 2B = 10/2/65; T = all transects.

Taxa	Transects	Sizes	No. Transects	No. Examined	Algae	Detritus	Animals
Platyhelminthes							
Dugesia	1-2A, 2B	All	22	15	96.04	3.96	0
Hirudinea	2B	All	1	1	20.47	79.53	0
Oligochaeta							
Branchiobdellidae	1-2B	All	28	14	0	0	100.00
Naididae and Tubificidae*	T	All	616	136	76.59	23.41	0
Hydracarina	T	All	44	9	30.38	69.62	0
Decapoda							
Cambarus robustus	T	2	1	1	1.10	0.39	98.52
		3	2	2	1.22	0.31	98.47
		4	3	3	38.26	4.85	56.89
		2-4	6	6	3.18	0.56	96.26
Orconectes obscurus	T	1	2	2	0.50	0.65	98.85
		2	1	1	1.56	0.81	97.62
		1-2	3	3	0.81	0.69	98.50
Plecoptera							
Chloroperla sp. 1	3A, 2B	2	4	4	0.37	0.37	99.31
		3	3	3	0.55	0.14	99.31
		2-3	7	7	0.44	0.25	99.31
Taeniopteryx maura	2A, 3A	3	26	11	0.24	1.16	98.60
		4	1	1	0.25	0.59	99.16
		3-4	27	12	0.24	1.01	98.75
Acroneturia lycorias	3A, 1-2B	1	7	3	100.00	0	0
		2	30	16	1.36	0.24	98.40
		3	2	2	0.27	0.07	99.66
		1-3	39	21	0.83	0.16	99.01
Phasganophora capitata	1-2B	3	3	3	1.88	0.35	97.77
		4	3	3	0.52	0.08	99.40
		3	6	6	1.62	0.30	98.08
Undet Plecoptera	2B	2	7	7	35.43	64.57	0
Ephemeroptera							
Centroptilum album	1-3A, 1-2B	1	82	29	86.74	13.26	0
		2	426	139	84.70	15.30	0
		3	83	59	39.19	18.81	0
		4	57	30	88.12	11.88	0
		5	32	19	90.42	9.58	0
		1-5	680	276	87.74	12.26	0

* The following species have been lumped: Allonais paragnayensis, Nais behningi; Limnodrilus hoffmeisteri and Rhyacodrilus montanus.

Taxa	Transects	Sires	No./ Transects	No. Examined	Algae	Detritus	Animals
Pseudocloeon sp.	2A, 1B	4	4	3	96.58	3.42	0
		5	5	3	32.89	6.11	0
		3	3	3	99.21	0.79	0
		3-5	12	9	98.81	1.19	0
Caenis anceps	1, 3A	2	5	3	100.00	0	0
		4	1	1	83.14	16.86	0
		5	1	1	93.62	6.38	0
		2, 4-5	7	5	92.14	7.86	0
Ephemerella simulans	2-3A, 2B	1	1	1	10.64	89.36	0
		2	8	8	1.15	3.40	95.45
		3	1	1	7.13	20.46	72.41
		1-3	10	10	3.30	9.82	86.88
Ephemerella varia	3A, 2B	2	11	10	80.24	19.76	0
		3	6	5	82.66	17.07	0.26
		4	1	1	83.21	16.79	0
		2-4	18	16	82.35	17.44	0.21
Ephemerella aestiva	2B	3	6	5	73.66	26.34	0
		4	2	1	59.81	40.19	0
		3-4	8	6	69.35	30.65	0
Ephemerella dorothea	1A, 2A	2	1	1	100.00	0	0
		4	1	1	9.02	90.98	0
		5	1	1	81.70	18.30	0
		2, 4-5	3	3	49.44	50.56	0
Stenonema canadense	1A, 3A, 2B	1	15	9	68.12	31.88	0
		2	35	26	88.75	11.25	0
		3	1	1	100.00	0	0
		5	2	2	82.40	17.60	0
		1-3, 5	53	38	86.60	13.40	0
Stenonema fuscum	1-3A, 1-2B	1	10	9	27.11	72.89	0
		2	37	21	78.63	21.37	0
		3	48	36	89.01	10.99	0
		4	23	20	86.97	5.70	7.33
		5	28	19	69.84	13.47	16.69
		1-5	146	105	80.48	9.51	10.01
Stenonema tripunctatum	1-3A, 1-2B	1	67	36	89.06	10.94	0
		2	66	48	86.73	13.27	0
		3	21	10	93.53	6.47	0
		4	10	8	89.92	9.67	5.41
		5	6	6	71.24	15.98	12.79
		1-5	170	108	78.61	13.09	8.30
Undet Stenonema	1-3A, 1-2B	1	151	63	73.62	26.38	0
		2	20	8	65.11	34.89	0
		3	12	6	65.78	34.22	0
		4	3	3	73.41	26.59	0
		1-4	186	80	70.40	29.60	0
Choroterpes sp.	2A	3	1	1	86.61	13.39	0
		4	1	1	69.78	30.22	0
		3-4	2	2	78.37	21.63	0
Habrophlebioides americana	1-3A, 1-2B	1	80	29	25.57	74.43	0
		2	170	88	27.84	72.16	0
		3	310	168	66.52	33.48	0
		4	55	42	73.63	26.37	0
		5	5	3	7.58	92.42	0
		1-5	626	330	49.13	50.87	0

Taxa	Transects	Sizes	No. Transects	No. Examined	Algae	Detritus	Animals
<i>Isorychnia albomaculata</i>	3A, 1-2B	2 3 4 5 2-5	15 12 4 2 33	9 7 4 2 22	32.26 51.97 50.60 23.12 25.82	67.71 48.03 49.40 13.73 17.52	0 0 0 63.15 56.66
Undet <i>Ephemeroptera</i>	1A, 1B	1 1	6 6	4 4	46.11 46.11	53.89 53.89	0 0
<i>Megaloptera</i> <i>Nigronia serricornis</i>	1-3A, 1-2B	1 2 3 4 5 1-5	22 32 6 2 10 72	20 25 6 2 10 63	4.89 0.38 3.66 1.88 3.23 3.45	1.58 1.21 0.95 1.82 1.00 1.12	93.53 94.97 95.39 96.30 95.77 95.43
<i>Sialis</i> sp.	1A, 1-2B	1 2 3 5 1-3, 5	2 7 4 3 16	2 7 6 3 15	1.70 4.35 0.07 3.91 3.50	0.91 0.86 0.04 0.71 0.68	97.39 94.79 99.89 95.38 95.82
<i>Trichoptera</i> <i>Goera calcarata</i>	3A, 1-2B	2 3 4 5 2-5	24 34 11 11 80	19 26 9 9 63	92.65 97.57 96.37 98.94 98.80	7.35 2.43 3.63 1.06 1.20	0 0 0 0 0
<i>Glossosoma nigrilor</i>	1-3A, 1-2B	1 2 3 4 5 1-5	54 204 219 115 58 650	13 64 49 55 30 211	89.99 99.34 98.42 96.31 98.53 98.36	10.01 0.66 1.58 3.69 1.47 1.64	0 0 0 0 0 0
<i>Helicopsyche borealis</i>	1-3A, 1-2B	1 2 3 4 1-4	19 288 132 82 521	4 68 39 24 135	100.00 32.37 96.10 96.32 66.59	0 1.41 3.90 3.68 2.69	0 66.22 0 0 30.72
<i>Cheumatopsyche</i> sp.	1-3A, 1-2B	2 3 4 5 2-5	1330 387 130 9 1856	470 246 97 9 822	52.30 43.74 38.46 75.52 50.41	10.90 7.03 6.03 9.29 7.22	36.80 49.23 55.51 15.19 42.37
<i>Hydropsyche betteni</i>	1, 3A, 1-2B	2 3 4 2-4	24 22 6 52	11 13 5 29	1.11 1.08 2.66 1.66	0.34 0.49 0.92 0.64	98.55 98.43 96.42 97.75
<i>Hydropsyche bronta</i>	1-3A, 1-2B	2 3 4 5 2-5	54 143 82 35 314	23 104 64 24 215	3.98 14.52 26.81 51.28 38.99	1.73 3.22 5.03 7.44 6.17	92.29 82.26 68.16 41.28 54.84

Taxa	Transects	Sizes	No. Transects	No. Examined	Algae	Detritus	Animals
<i>Hydropsyche</i> <i>glossonae</i>	1-3A, 1-2B	2	389	199	11.97	2.22	85.81
		3	477	334	15.41	3.49	81.10
		4	117	90	9.12	2.08	88.80
		5	13	13	22.26	2.62	75.12
		2-5	996	636	17.97	2.51	79.52
Undet <i>Hydropsychidae</i> sp.	1B	2	349	40	84.46	15.54	0
		2	349	40	84.46	15.54	0
<i>Pycnopsyche</i> <i>antica</i>	3A, 1B	1	3	2	30.06	69.94	0
		2	1	1	0.47	99.53	0
		1,2	4	4	9.02	90.98	0
<i>Neophylax</i> <i>nacatus</i>	1B	1	1	1	100.00	0	0
Undet <i>Limnephilidae</i>	3A	1	3	2	97.87	2.13	0
		2	1	1	97.90	2.10	0
		1-2	4	3	97.89	2.11	0
<i>Psilotreta</i> <i>indecisa</i>	1-3A, 1-2B	1	15	4	95.62	4.18	0
		2	120	43	51.46	5.36	43.18
		3	31	16	98.01	1.99	0
		4	27	18	98.52	1.30	0.18
		5	111	57	96.12	3.18	0.70
		1-5	304	138	96.99	2.30	0.71
<i>Gnmarra</i> <i>aterrima</i>	2-3A, 1-2B	1	2	1	91.75	8.25	0
		2	60	17	96.13	3.87	0
		3	144	41	85.07	14.93	0
		4	132	53	95.75	4.25	0
		5	82	38	54.97	39.61	5.42
		1-5	420	150	64.51	31.36	4.13
<i>Nyctiophylax</i> sp.	1A, 1-2B	2	2	2	0.22	0.26	99.52
		4	4	4	0.04	0	99.96
		5	6	5	4.99	1.88	93.13
		2, 4-5	12	11	1.14	0.51	98.35
<i>Polycentropus</i> <i>confusus</i>	1-3A, 1-2B	1	31	8	0	0	100.00
		2	37	27	0.03	1.12	99.85
		3	106	86	0.02	0.13	99.85
		4	38	32	0.15	0.33	99.52
		5	3	3	0.11	0.04	99.85
		1-5	215	156	0.09	0.09	99.82
<i>Psychomyia</i> <i>flavida</i>	1-3A, 1-2B	1	28	4	100.00	0	0
		2	264	28	94.93	5.07	0
		3	388	78	93.02	6.98	0
		4	375	189	95.29	3.29	1.42
		5	268	166	92.85	4.90	2.24
		1-5	1323	465	94.40	4.06	1.54

Taxa	Transects	Sizes	No./ Transects	No. Examined	Algae	Detritus	Animals
Diptera							
Palpomyia spp.	1, 3A, 1-2B	2	68	15	0	100.00	0
		3	148	33	9.12	90.88	0
		4	192	78	13.74	86.26	0
		5	99	30	0.65	99.35	0
		2-5	507	156	4.73	95.27	0
Cryptochironomus vulneratus	1B	3	1	1	57.25	42.75	0
Cryptochironomus sp. A	1A, 1B	2	1	1	4.26	95.74	0
		3	2	2	57.25	42.75	0
		4	2	2	33.16	66.84	0
		2-4	5	5	6.23	93.77	0
Cryptochironomus sp. B	1A	4	1	1	100.00	0	0
Cryptochironomus sp. C	1B	4	2	2	0.21	0	99.79
Cryptochironomus sp. 3	1A, 1B	5	4	4	0.07	0.07	99.86
Limnochironomus modestus	1, 3A, 2B	1	1	1	100.00	0	0
		3	10	8	72.61	27.39	0
		4	7	4	91.75	8.25	0
		5	1	1	10.04	89.96	0
		1, 3-5	19	14	87.14	12.86	0
Microtendipes pedellus	1-3A, 1-2B	1	17	16	30.69	69.31	0
		2	125	102	82.94	17.06	0
		3	29	26	84.18	15.82	0
		4	85	70	87.28	12.72	0
		5	131	88	87.20	12.80	0
		1-5	387	302	86.98	13.01	0
Paratendipes altimanus	1A	3	1	1	85.19	14.81	0
Phaenopsectra junducus	1, 3A, 1B	4	7	2	85.94	14.06	0
		5	2	2	91.64	8.36	0
		4-5	9	4	87.12	12.88	0
Phaenopsectra obediens	2A	5	1	1	43.35	56.65	0
Polypedilum fallax group sp. 1, 3A, 1B		3	5	3	0.51	0.03	99.46
		4	21	19	79.78	20.22	0
		5	2	2	81.06	18.94	0
		3-5	28	24	5.41	1.26	93.32
Polypedilum sp. nr. sordens	1A, 1-2B	4	34	31	83.88	16.12	0
		5	14	13	80.40	19.60	0
		4-5	50	45	82.70	17.30	0
Polypedilum scalaeum	1-3A, 1-2B	1	92	26	87.67	12.33	0
		2	76	45	77.36	22.64	0
		3	131	67	89.43	15.57	0
		4	17	17	81.32	18.68	0
		5	13	10	88.13	11.87	0
		1-5	329	165	84.62	15.38	0

Taxa	Transects	Sizes	No. / Transects	No. Examined	Algae	Detritus	Animals
<i>Tanytarsus</i> <i>conversus</i>	1A, 1-2B	2	2	2	86.75	13.25	0
		3	7	6	93.33	6.67	0
		4	14	14	83.45	16.55	0
		5	1	1	54.35	45.65	0
		2-5	24	23	83.74	16.26	0
<i>Tanytarsus</i> <i>exigua</i>	1-3A, 1-2B	1	2195	163	69.11	30.89	0
		2	3584	496	66.47	33.53	0
		3	994	324	67.28	32.72	0
		4	996	469	66.18	24.82	9.00
		5	30	6	35.36	64.64	0
		1-5	7799	1458	66.16	26.92	6.92
<i>Tanytarsus</i> sp. nr. <i>exigua</i>	1-2A, 1B	3	11	4	100.00	0	0
		4	6	5	64.62	35.38	0
		5	12	9	83.73	16.27	0
		3-5	29	18	73.67	26.33	0
<i>Tanytarsus</i> sp. nr. <i>polita</i>	1-3A, 1-2B	1	16	12	52.50	47.50	0
		2	40	30	70.92	29.08	0
		3	3881	338	82.69	17.31	0
		4	144	64	78.31	21.69	0
		5	693	205	79.20	18.54	2.26
		1-5	4747	651	79.76	19.08	1.16
<i>Tanytarsus</i> sp. 3	1A, 1B	4	1	1	65.92	34.08	0
		5	9	5	88.11	11.89	0
		4-5	10	6	87.20	12.80	0
<i>Tanytarsus</i> sp. 4	3A, 1B	3	7	7	62.08	37.92	0
		4	3	3	45.26	54.74	0
		3-4	10	10	46.88	53.12	0
<i>Tanytarsus</i> sp. 5	1A	5	1	1	100.00	0	0
<i>Stompellina</i> sp. nr. <i>phannseni</i>	1A, 2B	5	2	2	85.98	14.02	0
<i>Zavrelia</i> sp. nr. <i>pentatomal</i>	3A, 1-2B	1	5	5	100.00	0	0
		2	93	71	23.14	76.86	0
		3	126	102	18.43	7.42	74.15
		4	221	190	75.58	24.42	0
		5	22	15	57.39	42.61	0
		1-5	467	383	60.56	27.10	12.34
<i>Brillia flavifrons</i>	3A	1	3	2	3.59	96.41	0
		2	2	3	100.00	0	0
		3	3	2	49.55	50.45	0
		1-3	8	7	42.23	57.77	0
<i>Corynoneura taris</i>	1-3A, 1-2B	3	83	27	78.89	21.11	0
		4	247	22	72.49	27.51	0
		3-4	330	49	77.38	22.62	0
<i>Corynoneura</i> sp.	1-3A, 1-2B	2	158	19	58.77	41.23	0
		3	222	62	83.84	16.16	0
		4	189	66	59.62	40.38	0
		5	4	3	95.77	4.23	0
		2-5	583	199	66.18	33.82	0

Taxa	Transects	Sizes	No./ Transects	No. Examined	Algae	Detritus	Animals
Gen. nr.							
Corynoneura sp. 1-3A, 1-2B	1	141	63	100.00	0	0	
	2	284	135	98.23	1.77	0	
	3	53	31	42.06	57.94	0	
	4	72	28	66.18	33.82	0	
	5	25	21	79.65	20.35	0	
	1-5	575	278	67.65	32.35	0	
Cricotopus exilis 1-3A, 1-2B	1	71	6	100.00	0	0	
	2	195	19	95.72	4.28	0	
	3	325	79	97.67	2.33	0	
	4	145	67	88.88	11.12	0	
	5	5	2	84.50	15.50	0	
	1-5	741	173	93.94	6.06	0	
Cricotopus sp.							
nr. junus 3A, 1B	3	10	5	94.24	5.76	0	
	4	2	2	100.00	0	0	
	3-4	12	7	94.89	5.11	0	
Undet							
Cricotopus 1A, 2B	1	3	8	100.00	0	0	
	3	4	1	100.00	0	0	
	4	141	1	100.00	0	0	
	1, 3-4	144	10	100.00	0	0	
Eukiefferiella sp.							
nr. brevinervis 2-3A, 2B	3	32	4	100.00	0	0	
	4	2	1	98.70	1.30	0	
	3-4	34	5	99.42	0.58	0	
Eukiefferiella sp.							
nr. longicalcar 1B	3	1	1	100.00	0	0	
Eukiefferiella sp.							
nr. sordens 3A, 1-2B	2	18	4	100.00	0	0	
	3	27	9	81.06	18.94	0	
	4	9	4	100.00	0	0	
	2-4	54	17	81.31	18.69	0	
Eukiefferiella sp. 2 1-3A, 1-2B	1	100	9	28.77	71.23	0	
	2	193	34	30.20	69.80	0	
	3	206	76	60.37	39.63	0	
	5	17	8	42.22	57.78	0	
	1-3, 5	516	128	57.33	42.67	0	
Gen. nr.							
Eukiefferiella 1-3A, 1-2B	2	3	3	79.92	27.08	0	
	3	431	146	70.47	29.53	0	
	4	546	138	77.45	15.90	6.65	
	5	6	5	80.73	19.27	0	
	2-5	986	292	76.74	18.29	4.98	
Hydrobaenus sp.							
nr. paradoreus 1+3A, 1-2B	3	2	2	89.62	10.38	0	
	4	2	2	100.00	0	0	
	3-4	4	4	90.15	9.85	0	
Gen. nr.							
Metriocnemus 1-3A, 1-2B	1	21	13	46.32	53.68	0	
	2	55	28	56.30	43.70	0	
	3	54	35	68.95	31.05	0	
	4	49	37	84.86	15.14	0	
	5	47	35	81.26	18.74	0	
	1-5	226	148	80.30	19.70	0	

Taxa	Transects	Sizer	Transects	No. Examined	Algae	Detritus	Animals	35
<i>Psectrocladius</i> sp. nr. 4	2A, 1-2B	2	32	9	82.00	18.00	0	
		3	22	12	60.51	39.49	0	
		4	13	9	85.83	14.17	0	
		5	4	3	83.50	16.50	0	
		2-5	71	33	79.98	20.02	0	
<i>Trichocladus</i> sp. nr. 3	1-3A, 1-2B	2	3	3	69.06	30.94	0	
		3	23	19	7.05	4.54	88.41	
		4	12	9	82.41	17.59	0	
		5	5	3	25.77	74.23	0	
		2-5	43	34	13.14	9.87	76.99	
<i>Pentaneura</i> <i>auriensis</i>	1A	5	2	1	0.01	0	99.99	
<i>Pentaneura carnea</i> group sp.	1-3A, 1-2B	2	34	13	0.06	0	99.94	
		3	63	34	0.09	0.01	99.90	
		4	9	7	0.03	0	99.97	
		5	4	2	0.04	0	99.96	
		2-5	108	56	0.05	0	99.95	
<i>Pentaneura melanops</i> group sp.	1-3A, 1-2B	1	163	21	0.05	0.01	99.94	
		2	355	99	0.02	0.02	99.96	
		3	276	133	0.08	0.87	99.05	
		4	42	29	0.12	0.07	99.81	
		5	36	26	0.09	0.04	99.87	
		1-5	872	308	0.07	0.17	99.76	
<i>Pentaneura</i> <i>pilsella</i>	1-2A	2	714	4	0.06	0.05	99.89	
<i>Pentaneura</i> sp. A	1A	3	1	1	0	0	100.00	
Undet								
<i>Pentaneura</i>	1B	2	37	11	0	0	100.00	
<i>Procladius</i> sp. nr. adumbratus	1A	3	2	2	0	0	100.00	
<i>Hemerodromia</i> sp.	3A, 1-2B	1	197	62	43.87	56.13	0	
		2	236	90	36.32	63.68	0	
		3	44	21	34.24	65.76	0	
		4	20	7	26.11	73.89	0	
		1-4	497	170	34.20	65.80	0	
<i>Simulium</i> <i>venustum</i>	2-3A, 1B	2	21	8	84.45	15.55	0	
		3	30	18	92.93	70.73	0	
		4	3	3	37.61	62.39	0	
		2-4	54	29	89.93	10.07	0	
<i>Tabanus</i> sp.	1, 3A	2	1	1	99.30	0.70	0	
		5	1	1	0	100.00	0	
		2, 5	2	2	73.64	26.36	0	
<i>Antocha</i> sp.	1-3A, 1-2B	2	419	139	91.88	8.12	0	
		3	288	188	82.00	4.20	13.80	
		4	239	174	95.07	3.79	1.14	
		5	23	21	94.12	5.88	0	
		2-5	969	522	93.00	4.70	2.30	
<i>Dicranota</i> sp.	1A, 2B	4	9	4	20.03	79.97	0	
		5	2	2	100.00	0	0	
		4-5	11	6	22.50	77.50	0	

Taxa	Transects	Sizes	No./ Transects	No. Examined	Algae	Detritus	Animals
<i>Eriocera</i> <i>fultonensis</i>	1-2B	1	13	10	76.89	23.11	0
		2	10	4	0.30	0.07	99.63
		3	4	4	4.55	5.86	89.59
		1-3	27	18	1.95	1.90	96.15
<i>Tipula</i> sp.	1, 3A, 1-2B	1	1	1	100.00	0	0
		4	2	2	64.26	35.74	0
		5	3	3	7.13	15.48	77.39
		1, 4-5	6	6	8.46	15.94	75.66
Undet Diptera	1-2B	1	8	8	100.00	0	0
		2	24	7	100.00	0	0
		1-2	32	15	100.00	0	0
Coleoptera							
<i>Helichus</i> sp. 1	3A	adult	2	1	26.31	73.69	0
<i>Dubiraphia</i> sp.	3A	adult	13	5	26.11	73.89	0
<i>Optioservus</i> sp.	1-3A, 1-2B	1	38	7	85.02	14.98	0
		2	293	62	76.00	24.00	0
		3	458	152	91.07	8.93	0
		4	515	159	89.60	7.96	2.44
		5	248	133	89.78	10.22	0
		adult	52	22	75.51	24.39	0
		1-5	1552	513	89.63	9.39	0.98
<i>Stenelmis</i> <i>boamari</i>	1-3A, 1-2B	2	269	70	74.03	25.97	0
		3	425	175	15.03	4.62	80.35
		4	88	47	80.96	19.04	0
		5	99	61	93.59	4.72	1.69
		adult	62	23	59.35	40.65	0
		2-5	883	355	71.25	7.25	21.50
<i>Ectoparia</i> sp.	3A	3	2	2	98.79	1.20	0.01
		4	2	2	99.17	0.83	0
		2-4	4	4	98.95	1.05	0.01
<i>Psephenus</i> <i>herricki</i>	1-3A, 1-2B	1	28	10	100.00	0	0
		2	216	120	84.76	15.24	0
		3	56	20	96.65	3.35	0
		4	70	38	97.03	2.97	0
		5	28	24	98.47	1.53	0
		1-5	398	212	97.73	2.27	0
Mollusca							
<i>Ferrissia</i> <i>rivularis</i>	1-3A, 1-2B	1	11	8	87.74	12.26	0
		2	51	28	84.28	4.96	10.76
		3	39	15	97.49	2.51	0
		4	28	19	95.07	4.93	0
		5	11	10	96.21	3.79	0
		1-5	140	80	94.85	3.98	1.17
<i>Physa</i> sp.	2-3A, 1-2B	1	4	4	90.15	9.85	0
		2	3	3	65.02	34.98	0
		1-2	7	7	72.89	27.11	0

Taxa	Transects	Sizes	No./ Transects	No. Examined	Algae	Detritus	Animals	27
Sphaerium sp.	1-3A, 1-2B	2	3	2	27.06	72.94	0	
		3	1	1	95.72	4.28	0	
		4	4	4	74.31	25.69	0	
		2-4	8	7	77.52	22.48	0	
Pisces								
Cottus bairdii	1-2A, 1-2B	2	6	6	3.62	0.61	95.77	
		3	5	5	1.39	0.32	98.29	
		4	1	1	11.08	0.10	88.82	
		2-4	12	12	2.58	0.40	97.02	

Table 13. The standing crop calories (Λ_2 = algal consumption, $\Lambda_{2'}$ = detrital consumption, Λ_{3-n} = animal consumption) in each sample maintained by equal numbers of calories of the three food items and the per cent contribution of each food type. Data are presented for each sample with the macropredator standing crop distributed equally. All values are per square meter ($900 \text{ cm}^2 \times 11.1$).

Transect	Sample	Λ_2	% total	$\Lambda_{2'}$	% total	Λ_{3-n}	% total
1A	1	4,698	7.55	1,008	1.62	56,528	90.83
	2	8,115	12.24	1,379	2.08	56,821	85.68
	3	7,496	11.47	1,336	2.04	56,525	86.47
	4	13,165	18.22	1,907	2.64	57,198	79.14
	5	8,417	11.27	2,865	3.84	63,398	84.89
2A	1	8,614	24.24	1,763	5.02	25,140	70.74
	2	4,392	14.78	991	3.34	24,325	81.88
	3	5,506	18.37	1,095	3.65	23,365	77.97
	4	5,248	17.49	903	3.03	23,684	79.38
3A	1	9,219	23.27	861	2.17	29,533	74.55
	2	13,804	26.32	3,291	6.27	35,353	67.41
	3	27,484	33.58	7,453	9.11	46,900	57.31
	4	10,955	17.75	2,558	4.14	48,220	78.11
	5	7,016	13.81	6,635	13.06	37,151	73.13
1B	1	73,316	19.41	13,451	3.56	290,972	77.03
	2	67,964	18.57	11,103	3.03	286,832	78.39
	3	74,004	2.43	11,463	3.76	385,732	93.81
	4	76,174	20.19	12,883	3.41	288,310	76.40
	5	74,280	19.65	12,164	3.22	291,632	77.14
2B	1	21,522	21.52	5,153	5.15	73,323	73.32
	2	20,150	18.47	7,335	6.72	81,620	74.81
	3	27,812	24.90	4,622	4.17	79,280	70.97
	4	26,862	24.20	4,345	3.91	79,810	71.89
	5	28,392	25.23	7,103	6.31	77,050	68.46

Table 14. The impact of the macroconsumers ($\Lambda_{3-n}, \Lambda_2, \Lambda_2'$) on the standing crops of their foods ($\Lambda_2 + \Lambda_2'$, = prey; Λ_1 = algae, Λ_1' = detritus). The per cent impact is presented for some expected feeding rates: instantaneous X 24 = once every 60 minutes; X 48 = once every 30 minutes; X 12 = once every 120 minutes

Transect	Standing crop of Λ_1 in gram calories	Instantaneous caloric ingestion of Λ_1 by Λ_2	Instantaneous ingestion		Impact on Λ_1 by Λ_2 as % of total	
			X 24	X 48	Instantaneous	X 24 X 48
1A	1,822,000	451	10,824	21,648	0.02	0.59 1.18
2A	517,000	164	3,936	7,872	0.03	0.76 1.52
3A	152,000	995	23,880	47,760	0.65	1.57 3.14
1B	465,000	1,067	25,608	51,216	0.23	5.51 11.01
2B	249,000	3,779	90,696	181,392	1.52	36.42 72.85

Transect	Standing crop of Λ_1 in gram calories	Instantaneous caloric ingestion of Λ_1 by Λ_2'	Instantaneous ingestion		Impact on Λ_1 by Λ_2' as % of total	
			X 24	X 48	Instantaneous	X 24 X 48
1A	57,000	42	1,008	2,016	0.07	1.77 3.54
2A	45,000	15	360	720	0.03	0.80 1.60
3A	174,000	250	6,000	12,000	0.14	3.45 6.90
1B	3,000	117	2,808	5,616	3.90	93.60 187.20
2B	108,000	131	3,144	6,288	0.12	2.91 5.82

Table 14. (continued). The impact of the macroconsumers ($\Lambda_{3-n}, \Lambda_2, \Lambda_1$) on the standing crops of their foods ($\Lambda_2 + \Lambda_1, \Lambda_1, \Lambda_2$). The per cent impact is presented for some expected feeding rates: instantaneous $\times 24$ = once every 60 minutes; $\times 48$ = once every 30 minutes; $\times 12$ = once every 120 minutes.

Transect	Standing crop of $\Lambda_2 + \Lambda_1$, with the macropredators included	Instantaneous caloric ingestion by $\Lambda_2 + \Lambda_1$, by Λ_{3-n}	Instantaneous ingestion $\times 12$	Impact on $\Lambda_2 + \Lambda_1$, as % of total	by Λ_{3-n}
1A	10,077	971	11,652	9.64	115.63
2A	7,133	153	1,836	2.14	25.74
3A	17,856	1,469	17,628	8.23	98.72
1B	85,361	1,350	16,200	1.58	18.98
2B	30,660	1,340	16,080	4.37	52.45

Transect	Standing crop of $\Lambda_2 + \Lambda_1$, with the macropredators excluded	Instantaneous caloric ingestion of $\Lambda_2 + \Lambda_1$, by Λ_{3-n}	Instantaneous ingestion $\times 12$	Impact on $\Lambda_2 + \Lambda_1$, as % of total	by Λ_{3-n}
1A	9,064	533	6,396	5.88	70.53
2A	6,253	141	1,692	2.22	27.06
3A	17,437	1,011	12,132	5.80	69.58
1B	23,309	703	8,436	3.02	36.19
2B	27,146	847	10,164	3.12	37.44

Table 15. Calculated assimilation rates for each macroconsumer level based on either a 30 day or a 7 day turnover time of the standing crops. (Growth is assumed to be 30% and respiration 70% of assimilation.)

Transect	Trophic Placement	Standing crop (cal/m ²)	Standing crop turnover/day (cal/m ² /day)		Respiration (cal/m ² /day)		Assimilation/m ² /day (i.e. turnover/day + respiration/day)	
			Assuming a turnover time in days of:		Assuming a turnover time in days of:		Based on a turnover time in days of:	
			30	7	30	7	30	7
1A (Aug. 2, 1964)	A 3-n	2,296	77	328	179	765	356	1,093
	A 2 + 2'	9,069	302	1,296	705	3,024	1,007	4,320
	A 2	7,634	254	1,091	593	2,546	847	3,637
	A 2'	1,435	48	205	112	478	160	683
2A (Sept. 1, 1964)	A 3-n	2,459	82	351	191	819	273	1,170
	A 2 + 2'	6,253	208	893	485	2,084	693	2,977
	A 2	5,145	172	735	401	1,715	573	2,450
	A 2'	1,108	37	158	86	369	123	527
3A	A 3-n	10,911	364	1,559	849	3,638	1,213	5,197
	A 2+2'	17,437	581	2,491	1,356	5,812	1,937	8,303
	A 2	13,342	445	1,096	1,038	2,257	1,483	3,353
	A 2'	4,095	137	585	320	1,365	457	1,950
1B (Aug. 4, 1965)	A 3-n	6,264	209	895	486	2,088	697	2,983
	A 2+2'	23,309	777	3,330	1,813	7,770	2,590	11,100
	A 2	18,274	609	2,611	1,421	6,092	2,030	8,703
	A 2'	5,035	168	719	392	1,678	560	2,397
2B (Oct. 2, 1965)	A 3-n	9,467	316	1,352	737	3,155	1,053	4,507
	A 2+2'	27,148	905	3,878	2,112	9,049	3,017	12,927
	A 2	22,396	747	3,199	1,743	7,464	2,490	10,663
	A 2'	4,752	158	679	369	1,584	527	2,263

Table 16. Calculated Λ_{3-n} feeding rates and necessary prey turnover based on the initial assumption of either a 30 day or a 7 day turnover time of the standing crop.

Transect	Trophic Placement	Instantaneous ingestion (cal/m ²)		Gut turnover per day ¹		Feeding period ² (hours)		Ingestion per m ² per day		Prey turnover (days) ³	
		Assimil. 40%	Egest. 60%	100%	30	7	30	7	30	7	30
1A (Aug. 2, 1964)	Λ_{3-n}	221	332	553	1.2	4.9	20.0	4.9	664	2,710	13.6
	$\Lambda_{2+2'}$	194	292	486	5.2	22.3	4.6	1.1	2,527	10,837	3.3
	Λ_2	178	268	446	4.8	20.4	5.0	1.2	2,141	9,098	
	$\Lambda_{2'}$	16	24	40	10.0	42.7	2.4	0.6	400	1,708	
2A (Sept. 1, 1964)	Λ_{3-n}	46	85	141	5.9	25.4	4.1	0.9	832	3,581	1.7
	$\Lambda_{2+2'}$	70	105	175	9.9	42.5	2.4	0.6	1,733	7,438	
	Λ_2	64	96	160	9.0	32.3	2.7	0.7	1,440	5,168	
	$\Lambda_{2'}$	6	9	15	20.5	87.8	1.2	0.3	308	1,317	
3A (Oct. 7, 1964)	Λ_{3-n}	404	607	1,011	3.0	12.9	8.0	1.9	3,033	13,042	5.7
	$\Lambda_{2+2'}$	496	743	1,239	3.9	16.7	6.2	1.4	4,832	20,699	1.3
	Λ_2	396	594	990	3.7	8.5	6.5	2.8	3,663	8,415	
	$\Lambda_{2'}$	100	149	249	4.6	19.5	5.2	1.2	1,145	4,856	
1B (Aug. 4, 1965)	Λ_{3-n}	281	422	703	2.6	10.6	9.2	2.3	1,828	7,452	3.1
	$\Lambda_{2+2'}$	450	676	1,126	5.8	24.7	4.1	1.0	6,531	2,781	
	Λ_2	406	609	1,015	5.0	19.9	4.8	1.2	5,075	20,199	
	$\Lambda_{2'}$	44	67	111	12.7	54.5	1.9	0.4	1,410	6,050	
2B (Oct. 2, 1965)	Λ_{3-n}	339	508	847	3.1	13.3	7.7	1.8	2,626	11,265	2.4
	$\Lambda_{2+2'}$	1,560	2,339	3,899	1.9	8.3	12.6	2.9	7,408	32,362	
	Λ_2	1,509	2,663	3,772	1.7	7.1	14.1	3.4	6,412	26,781	
	$\Lambda_{2'}$	51	76	127	10.3	44.4	2.3	0.5	1,308	5,639	

1. Gut turnover/day = $\frac{\text{cal assimil/m}^2/\text{day}}{\text{inst. assimil/m}^2/\text{day}}$

2. Feeding period = time to clear gut in hours

3. Prey turnover = number of days for Λ_{3-n} to deplete prey standing crop = $\frac{\Lambda_{2+\Lambda_{2'}}}{\text{ingest/day by } \Lambda_{3-n}}$

Table 17. Calculated macroconsumer assimilation rates (based on previously stated assumptions of turnover time and assimilative and respiratory efficiencies).

Transect	Macroconsumer assimilation ($\Lambda_{3-n} + \Lambda_2 + \Lambda_{2'}$) (Kcal/m ²)						
	Assimil/m ² /day assuming a turnover time of		Assimil/m ² / mo (30 days) assuming a turnover time of		Assimil/m ² / yr (365 days) assuming a turnover time of		
	30	7	30	7	30	7	
1A (Aug. 2, 1964)	1.263	5.413	37.890	162.390	460.995	1975.745	
2A (Sept. 1, 1964)	.966	4.147	28.980	124.410	352.590	1513.655	
3A (Oct. 7, 1964)	3.150	13.500	94.500	405.000	1149.750	4927.500	
1B (Aug. 4, 1965)	3.287	14.083	98.610	422.490	1199.755	5140.295	
2B (Oct. 2, 1965)	4.070	17.434	122.100	523.020	1485.550	6363.410	
Fall Means	2.547	10.915	76.416	327.462	292.728	3984.121	